CLEANING SYMBIOSES BETWEEN HAWAIIAN REEF FISHES AND GREEN SEA TURTLES, *CHELONIA MYDAS*, WITH AND WITHOUT FIBROPAPILLOMAS

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAI'I IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN

ZOOLOGY

AUGUST 1999

George -
Thanks so much
for all your help over
the duration of this
project!!
All the best,
Jill

By

Jill P. Zamzow

Thesis Committee:

George S. Losey, Jr., Chairperson
Ernst S. Reese
David W. Greenfield

We certify that we have read this thesis and that, in our opinion, it is satisfactory in scope and quality as a thesis for the degree of Master of Science in Zoology.

THESIS COMMITTEE

Chairperson

ACKNOWLEDGEMENTS

I thank my thesis committee, G. S. Losey, E. S. Reese, and D. W. Greenfield, for considerable help and guidance in this endeavour. Field and technical assistance by G. H. Balazs, D. Ellis, S. Murakawa, T. Work, M. Rice, S. Hau and J. Fender is greatly appreciated. Data provided by M. Rice, P. Bennett, and U. Keuper-Bennett greatly improved the quality of this work. P. A. Nelson and N. J. Marshall were invaluable in reviewing the various drafts of this document. A. Taylor and P. A. Nelson speeded up my statistical analyses immeasurably by sharing their considerable knowledge with me. D. A. Copson Jr., E. C. Conklin, W. Loeffler, J. Coyer, and my family all went far beyond the call of duty in providing moral support for the duration of the study. Funding was graciously provided by the National Marine Fisheries Service and by the Lerner-Gray fund for marine research.

ABSTRACT

Green turtle fibropapillomatosis (GTFP), an infectious disease of probable viral etiology, is afflicting the green sea turtle worldwide. The most frequent fate of turtles afflicted with the disease is death. Cleaning symbioses between Hawaiian reef fishes and green sea turtles, *Chelonia mydas*, were studied at several sites around the Islands in order to determine any relationships between cleaning and GTFP, as well as to elucidate the nature of the cleaning symbiosis itself. Cleaning symbioses are often assumed to be mutualisms. This assumption has lately been challenged by a number of researchers studying a wide range of cleaning symbioses, including fish-fish, fish-turtle, fish-mammal, and bird-mammal interactions. Cleaning symbioses may categorized in a number of ways, e.g. by the behaviors of the participants and the food source exploited. Around the Hawaiian Islands, both of these vary with the location of occurrence. Behaviorally, cleaning symbioses between fish and turtles in the Hawaiian Islands were found to range from parasitic to possibly mutualistic interactions. If categorized by food utilization, grazing, a symbiosis in which fishes clean algae, bacteria, and detritus from the turtles' shells, was found to be the predominant form of cleaning. Kaneohe Bay, Oahu was found to be a unique cleaning environment, characterized by a paucity of grazing fishes; the main cleaner is *Thalassoma duperrey*, the saddleback wrasse, which feeds primarily on the turtle-specific parasitic skin barnacle *Platylepas hexastylos*. In some fish-fish cleaning symbioses, the cleaner targets damaged tissues or host mucus. This was not found in the Kaneohe Bay symbiosis: the wrasse did not feed preferentially on turtle tumors. *Thalassoma duperrey* fed most rapidly on the areas of the turtle with

the highest skin barnacle density. The wrasse displayed three different types of feeding bites, and used different types of bite when feeding on different areas of the turtle. Turtles flinched in response to cleaning bites different amounts depending on the feeding mode employed, and also depending on the species of cleaner. Honokowai, Maui was another unique cleaning environment where *Forcipiger flavissimus, Chaetodon miliaris* and *Ctenochaetus strigosus* are the main cleaners, and they focus cleaning bites on turtle tumors, not skin or barnacles. A number of tumor regressions have been documented from Honokowai, Maui; this might be due to amelioration by cleaner fishes. Cleaning symbiosis between Hawaiian reef fishes and green sea turtles seems to be a highly adaptable and changeable relationship.

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INTRODUCTION

Green turtle fibropapillomatosis (GTFP) is a debilitating and frequently fatal disease of the green sea turtle, *Chelonia mydas*, in geographic locations around the world. GTFP occurs in the Pacific Ocean, western Atlantic Ocean, Gulf of Mexico, Indian Ocean and the Caribbean Sea (Hendrikson 1958, Jacobson *et al.* 1989, MacDonald and Dutton 1990, Balazs 1991, Teas 1991, Ehrhart 1991, Limpus and Miller 1994, Williams *et al.* 1994, Aguirre *et al* 1999). The disease was first described over 60 years ago, in a turtle that had been captured near Key West, Florida (Lucke 1938, Smith and Coates 1938). GTFP has reached epidemic proportions in green turtle aggregations in Florida, Hawaii, Australia, and the Caribbean (Balazs *et al.* 1998). The first confirmed case of GTFP in the Hawaiian Islands occurred in a green turtle killed by fisherman in Kaneohe Bay, Oahu Island (Figures 1, 2) in 1958 (Balazs 1991). Over the past 10 years, the annual prevalence of afflicted turtles at this location fluctuated from 33 to 60% and is an ongoing problem (Balazs *et al.* 1998). This study attempts to elucidate any relationships between GTFP and cleaning symbioses in green turtle aggregations in the Hawaiian Islands.

Fibropapillomatosis is characterized by the formation of lobulated fibrous tumors on skin surfaces, in the eyes, and less frequently, on the internal organs (Harshbarger 1991, Jacobson *et al.* 1989, Norton *et al.* 1990, Herbst and Klein 1995). In Hawaiian green turtles the disease is unique and particularly damaging to turtles in that tumors also form in the oral cavity causing the obstruction of both breathing and the ingestion of food (Balazs 1991).

The etiology of fibropapillomatosis is unknown, but the disease has been conclusively demonstrated, through the use of tumor homogenates in captive turtle studies, to be transmissible and infectious (Herbst *et al.* 1995, 1996, Jacobson *et al.* 1991). A viral agent appears to be the responsible pathogen, and a herpesvirus, a retrovirus, and a papillomavirus are all implicated (Quackenbush *et al.* 1998, Lu 1998, Balazs *et al.* 1998, Casey *et al.* 1997). Whereas it is essential that the causal virus be isolated, identified and characterized, it is also of urgent importance that research concurrently is undertaken on the transmission between turtles. Knowledge of these aspects is essential in order to devise effective management plans to control or contain the disease.

Cleaning symbioses between marine turtles and various reef fishes that feed on organisms growing on the turtles' skin, scales, and carapace have been reported in the literature for a number of years (Booth and Peters 1972; Balazs 1980, 1995; Balazs *et al.* 1994, Smith 1988; Moll *et al.* 1995). A cleaning symbiosis was recently reported in which the Hawaiian saddleback wrasse, *Thalassoma duperrey*, picks the turtle-specific parasitic skin barnacle, *Platylepas hexastylos*, from the skin of the green sea turtle in Kaneohe Bay, Oahu Island, Hawaiian Islands (Losey *et al.* 1994, 1999). The turtles "pose," hanging motionless in the water column and extending neck, flippers, and tail for the cleaners' attention. At other locations around the Hawaiian Islands, anecdotal evidence suggests that cleaning of turtles by *T. duperrey* produces a painful "flinch" response and the turtle rapidly leaves the area, sometimes swatting at or attempting to bite the cleaner (Losey *et al.* 1994, 1999, JPZ pers. obs.). Cleaning symbioses between *Chelonia mydas* and *Thalassoma* species (Labridae) occur in at least three locations worldwide: Hawaii (Losey *et al.* 1994, 1999), Australia (Booth and Peters 1972), and Borneo (JPZ, pers. obs.).

The objectives of this work were twofold: first, to gain an increased understanding of these cleaning relationships and any correlation they may have with green turtle fibropapillomatosis. Reef fishes may serve as vectors for the disease as they move between turtles, or by causing wounds while cleaning may leave the turtle open for infection. Conversely, the cleaning behavior may serve a beneficial purpose in controlling ectoparasites and/or ameliorating tumor tissue. Increased information on these cleaning interactions between fishes and turtles is needed to determine if a significant impact exists, positively or negatively, with regard to green turtle fibropapillomatosis.

The second objective of this work was to determine whether the cleaning relationship taking place in Kaneohe Bay, Oahu, was different from the fish-turtle interactions seen elsewhere in the state, as Losey *et al.* (1994) implied. Cleaning symbioses, be they fish-fish, turtle-turtle, invertebrate-sponge, bird-mammal, or fish-mammal interactions, often are assumed to be mutualisms, with both participants benefiting from the interaction (Feder 1966, Swartz 1981, Hendler 1984, Poulin 1993, Mooring and Mundy 1996, Krawchuk 1997). Several authors, however, realized that this may not always, or often, be a correct assumption (Losey 1979, Zander and Neider 1997, Grutter and Poulin 1998). Cooperation between marine fishes and turtles, similarly, does not necessarily portend mutual benefit for the participants. Turtle cleaning may have two sides: a mutualistic relationship, as seen in Kaneohe Bay, Oahu I. and on the Kona Coast, Hawaii I. (Fig 1), and a commensal or even parasitic association, as seen at other locations around Hawaii (Losey *et al.* 1994, 1999, JPZ pers. obs.).

METHODS

Cleaner station monitoring

Daylight-hours monitoring of turtle cleaning sites was performed in Kaneohe Bay, Oahu Island, Hawaiian Islands from 1995 to 1999. Surveys took place at "Reef 42"(42), and at "Mark's Reef (MR)" (Figure 2). A remote video camera system was placed on the reef in the vicinity of a known turtle cleaning station, and was monitored from a small boat approximately 100m away. A pan and tilt mechanism allowed me to monitor 360 degrees around the camera within the limits of visibility. Videotape was recorded with a portable analog videocassette recorder whenever there was a turtle in view.

Six day-long surveys were also conducted, three each at 42 and MR. The remote video system was deployed and continually monitored from the surface during daylight hours (including pre-sunrise and post-sunset hours). Underwater time-lapse video was simultaneously recorded at resting sites in the vicinity of the target cleaning station. The time-lapse system was set to record 1second of footage per 5 minutes elapsed, and was deployed during daylight hours and left undisturbed for the life of the battery system (approximately eight hours).

Laboratory analysis

Real time video footage was analyzed with a behavioral event-recording software program (BEAST). Data were only used in statistical analyses if turtles were continuously within the camera's field of view for ≥120 seconds. For each cleaning encounter, the following events were recorded: individual turtle identity, tumor score (defined below), number of cleaning bites by *T. duperrey*, type of bite, location of bite on the turtle (front flippers, rear flippers/tail, head/neck, or shell), whether the bite(s) hit a tumor, reaction of the turtle to the bite, duration of herbivorous cleaning, and species of grazer present.

A "grazer" is defined for the purposes of this paper as a fish that is either a strict herbivore, or feeds on a combination of algae, diatoms, detritus, and bacteria, but not macroscopic invertebrate prey (Jones 1968, Hobson 1972). Duration of a cleaning encounter was measured as the period of time when there was both a turtle and a cleaner fish in the frame, and the cleaner was within at least 0.5 m of the turtle. The cleaner was most often actively inspecting the turtle or feeding (as described in Youngbluth 1968) and the turtle was often "posing" in the water column, extending its head and limbs and hanging motionless in the water column for the cleaner's inspection. A turtle's identity was ascertained by mapping carapace and plastron barnacles, tumors (if present), estimating size (small, medium, or large), noting tail length, and any abnormalities such as amputated flippers or other scars or marks. The number of tumors and their "class" was recorded; this was used to generate a "tumor score" for each individual (Table 1).

Table 1. Numbers of each size class of tumors used for placement into a particular tumor score category for green turtles afflicted with fibropapillomatosis in Hawaii (from Work and Balazs 1999).

		Overall Tumor Score			
Tumor Class	Maximum Tumor Diameter	0	1	2	3
		Number of tumors			
(A)	<1 cm	0	1-5	>5	>5
(B)	4 cm	0	1-5	>5	>5
(C)	10 cm	0	0	1-3	>3
(D)	>10 cm	0	0	0	≥1

Cleaning bites were assigned to one of three categories: "S-type," "C-type," and "T-type." S-type bites occurred when the fish closed its jaws on a parasite or the turtle's tissue, and then thrashed its body back and forth, describing an S-shaped motion. A twisting or rotation of the body sometimes accompanied this bite. A C-type bite was recorded when the fish bit the parasite or turtle with enough forward velocity that its body formed a "C" shape upon contacting the turtle. A T-type bite seemed to be an exploratory bite, characterized by the fish appearing to gently mouth the turtle, with no bending of the body.

For each resting encounter, individual turtles were identified as above, and the location of the particular resting site within the vicinity of the cleaner station was noted. BEAST was used to calculate duration of each resting period.

Mapping of Kaneohe Bay Cleaning Sites

Cleaning stations used during this study were mapped on a finer scale than can be found on nautical charts of the region. For purposes of mapping the Mark's Reef site

(Figure 3), I was elevated to a height of approximately 13m along the mast of the sailing vessel Desperado, and then proceeded to map the surrounding reef area manually. The map of Reef 42 (Figure 4) was adapted from a remote-sensing image furnished by Eric Hochberg, School of Ocean and Earth Science and Technology, University of Hawaii. Global positioning systems (GPS) coordinates of the cleaning sites were also taken.

Comparative Cleaning Sites

Six cleaning sites outside of Kaneohe Bay were surveyed as points of comparison to the Kaneohe Bay sites. Cleaning stations at Hanauma Bay, Oahu; Honokowai, West Maui; East Lanai; Honokohau, Island of Hawaii; Hilo, Island of Hawaii; and off of the Mauna Lani Hotel, Island of Hawaii were investigated with SCUBA and a hand-held underwater video camera. A survey was conducted along the Kona coast in order to investigate reports of cleaner stations given by University of Hawaii research divers. I was towed at slow speeds from Puako Point to Waima Point, and two snorkelers surveyed a small reef at Paniau.

Videotapes were analyzed (BEAST) to identify cleaner species and type of cleaning, individual turtle identity, location of bites taken by cleaner fishes, turtle reaction to cleaner bites, and whether cleaner bites hit a tumor. Hand-held videotape quality was often poor, depending on visibility and proximity to turtles, and sometimes could not be analyzed fully for these reasons. Supplemental videotape for analysis of Honokowai cleaners was provided by Ursula Keuper-Bennett and Peter Bennett (http: www.turtletrax.org), and supplemental Mauna Lani and Honokowai videotapes were provided by Marc Rice, Hawaii Preparatory Academy.

Survey of Dive Tour Operators

A survey of 15 dive tour operators around the state as well as 82 University of Hawaii certified academic research divers was undertaken in order to ascertain the number, approximate locations and seasonality (if any) of cleaning sites that are currently being encountered during diving activities around the islands. The survey was conducted via telephone, in-person, and electronic mail interviews.

Skin barnacle survey

A survey of parasitic skin barnacle load on twenty green turtles in Kaneohe Bay was performed on 14 through 16 October, 1997, and on 28 April 1999, in collaboration with the National Marine Fisheries Service (NMFS) Honolulu office. Green sea turtles were hand-captured from 42 or MR by snorkelers, or via NMFS personnel diving from the bow of a small boat onto a feeding turtle over Ahu o Laka sand bar (Figure 2). A clear plastic metric ruler was laid against the turtle's skin, and the number of barnacles falling totally or partially beneath this ruler, as well as the length of the skin of the given appendage, was recorded. Each appendage (flipper, neck, or tail) was surveyed via multiple "transects" with the ruler. Front flippers and neck were treated as a cylinder, and surveyed at 0 (top), 90, 180, and 270 degrees around this cylinder. The zero end of the ruler was placed at the skin/shell margin, and the distal termination of the transect was the skin/scale boundary. An initial survey, conducted at 45-degree intervals, indicated that the 90-degree survey would be sufficient in terms of variability of transects over each appendage. Rear flippers and associated skin area were counted by laying ruler transects along the anterior-to-posterior axis of the animal every 2 cm beginning at the shell/skin margin and ending at the edge of the tail. The tail was counted down the long axis of the ventral surface of the tail.

Gut content analysis and viral study

In August and September of 1998, *T. duperrey* were collected by spearing and/or with baited hook and line. Both spear and hook and line were wielded by a snorkeler in order to ascertain that the fish collected were within the geographical confines of the cleaning station on Reef 42, North Kaneohe Bay, Oahu. Fish were euthanized and gut contents were inspected in order to ascertain whether the individual fish was a cleaner. Presence or absence of turtle skin barnacles was noted and cleaners were then packed on ice and immediately delivered to Dr Yuanan Lu of the Retrovirology Research Center at Leahi Hospital, Honolulu for viral analyses.

Non-cleaner (control) *T. duperrey* were collected by snorkelers with baited hook and line in April 1999. These fish were collected from "Checker Reef," South Kaneohe Bay, Oahu, approximately two and three-quarters miles south of Reef 42, and one mile south of Mark's Reef (Figure 2). No turtles were seen on the surface or in the water at Checker Reef, and it is not known to be a turtle cleaning or resting site. Control fish were delivered alive, the morning after collection, for subsequent euthanization and viral screening.

Data analyses

Data were analyzed using Microsoft Excel 1997 and Minitab release 12.1. Data were transformed when necessary to meet assumptions of normality, or non-parametric methods were used if necessary.

To test for fish preference of tumored tissue on turtles, an estimation index was devised, based on Work and Balazs' (1999) tumor score ranking system (Table 1). The hypotheses tested were: 1) *T. duperrey* in Kaneohe Bay avoids tumors in its cleaning of tumored turtles, and 2) fishes at Honokowai, West Maui prefer to feed on tumors when cleaning tumored turtles. The area covered by tumors and by normal skin in each tumor score class was estimated. To avoid biasing my results, for Kaneohe Bay I used a conservatively low estimate for tumor surface area (based on the range given by Work and Balazs 1999), and high values for non-tumored skin surface area (based on actual skin area values from the barnacle survey). Honokowai estimates used conservatively high tumor area estimates and low non-tumored skin surface area estimates. Actual data were then compared with the estimated random distribution that would be expected, via a randomization test performed for 10,000 iterations.

A second set of randomization tests was performed in order to ask the question, "Do cleaner fish in Kaneohe Bay clean turtle tumors (versus skin) in the same proportion as do the fishes at Honokowai?" In order to test for this possible difference between Kaneohe Bay and Honokowai, the rate at which fish in Kaneohe Bay fed on tumors was used to set the probability of feeding on tumors for the fish at Honokowai. Using this Kaneohe Bay probability, "virtual cleaner" bites were randomly assigned to either skin or tumor of "virtual turtles" with tumor and skin surface areas calculated from the aforementioned estimation index. The same number of turtles of each tumor score (Table 1) that we have real data for at Honokowai was used, and tested for 10,000 iterations.

RESULTS

Cleaner station monitoring

Approximately 300 hours were spent in field observations of turtle cleaning stations in Kaneohe Bay, Oahu Island, Hawaiian Islands. Cleaning was observed at least once in every month of the year. A total of 42 hours (2520 minutes) of real-time video and 40.4 hours of observations by time-lapse video were reviewed; the duration of cleaning interactions totaled 553 minutes. Forty-two individual turtles were identified, 37 from cleaning bouts, three from resting bouts, and two from both types of interaction. At least 14 of these animals (33%) were afflicted with GTFP. Ninety-five turtle visits to the cleaning stations were analyzed, 10 from Mark's Reef, and 85 from Reef 42. These visits ranged from 25 seconds to 29 minutes in length. A total of 593 cleaning bites was taken by the Hawaiian saddleback wrasse, *T. duperrey* (Table 2). Two bites (one producing a flinch response) were taken by the whitespotted toby, *Canthigaster jactator; Labroides phthirophagous* was seen once, inspecting and picking at a turtle's shell. In addition, grazers (most often *Ctenochaetus strigosus* or schools of juvenile Scaridae and occasionally *Chaetodon miliaris* or *Acanthurus spp.*) spent a total of 119.8 minutes (21.6% of total cleaning observations) grazing on the turtles' shells and skin (Tables 2, 10). There was no significant difference found in duration of feeding by these grazing fishes (as a percentage of total cleaning time observed) between tumored and healthy individuals (Kruskal-Wallis: H=0.24, DF=1, p= 0.622).

Table 2. Summary of Observations of Turtle Cleaning Stations in Kaneohe Bay, Oahu

Turtle Condition	Individual turtles observed (N)	Total bites taken by *T. duperrey* (N)	Bites On Tumors (N)	Duration of grazing (not inc. *T. duperrey*): mean +/- s.d. (min)	Total time cleaning observed (min)
Tumored	14	316	30	1.03 +/- 2.62	254.6
Clean	28	277	N/A	1.63 +/- 3.03	298.7
Total	42	593	16	1.32 +/- 2.83	553.3

Within Kaneohe-Bay comparisons

Whether *T. duperrey* feeding bites fell on tumors or skin of turtles in Kaneohe Bay could not be distinguished from random, based on an ideal free distribution of bites between tumored and non-tumored tissues (randomization test based on estimation index, see Methods section; $p=0.19$ at 10,000 iterations). *Thalassoma duperrey* feeding rate (bites-per-minute cleaning observed) was significantly faster when feeding on the rear flippers than on the head and neck (Table 3, Tukey's post-hoc comparison $q=4.29$, $k=3$, $p<0.05$), but feeding rate did not differ significantly among the three tumor classes (TS=0, 1, >1, Table 1) of turtle (Tables 3).

Table 3. Two-way ANOVA of feeding rate by tumor score and location of feeding on turtle

Source of variation	Sum of Squares	Degrees of Freedom	Mean Squares	F-statistic	P-value
Factor Tumor Score	0.687	1	0.687	1.957	0.166
Factor Feeding Location	3.751	2	1.876	5.346	**0.007**
Tscore x Location interaction	0.459	2	0.229	0.653	0.523
Error	25.26	72	0.351		

Overall, in Kaneohe Bay, *T. duperrey* used the "S" mode of feeding significantly less often than the other two modes (Kruskal-Wallis H=15.00, DF=2, p=0.001.). When feeding mode is broken down by the health status of the turtle, however, the relationship does not hold for tumored turtles (Table 4). *Thalassoma duperrey* in Kaneohe Bay used the "C" mode and "T" modes of feeding similar amounts of time (Kruskal-Wallis H=1.41, DF=1, p=0.236 and see Table 4). *Thalassoma duperrey* used the "S" mode of feeding more often on tumored turtles, though this difference was not statistically significant (Table 4). *Thalassoma duperrey* occasionally took bites which did not clearly fall within the parameters of one of the feeding modes; these bites were recorded but not classified, hence the row totals do not equal 100%.

Table 4. Type of feeding bites taken by *T. duperrey* versus health of turtle in Kaneohe Bay.

	Median bites (% of total bites) employed by *T. duperrey*			
	S-type	C-type	T-type	Kruskal-Wallis: H(DF): p
Tumored (n=11)	20%	45%	20%	2.79(2): 0.248
Healthy (n=15)	6%	53%	35%	**13.92(2): 0.001**
Kruskal-Wallis: H(DF): p	3.3(1): 0.069	0.24(1): 0.622	0.04(1): 0.844	

T-type bites taken by *T. duperrey* in Kaneohe Bay were significantly more likely to land on the turtles' shells, and C-type bites were less likely to fall on the turtles' shells (Table 5). Often, location on the turtle or type of bite could not be definitively classified, hence row and column totals do not equal 100%

Table 5. Comparisons between feeding location and method of feeding employed by *Thalassoma duperrey* in Kaneohe Bay, Oahu Island, for turtles with and without fibropapillomas

	Median % of bites on specific turtle area by *T. duperrey*		
Tumored turtle area:	S-type	C-type	T-type
Shell	0%	0%	99%
Front flippers & neck	38%	30%	0%
Rear flippers & tail	38%	28%	0%
Kruskal-Wallis H(DF): p	2.6(2): 0.263	**6.09(2): 0.048**	**11.74(2): 0.003**
Healthy turtle area:			
Shell	0%	0%	53%
Front flippers & neck	0%	24%	15%
Rear flippers & tail	48%	35%	7%
Kruskal-Wallis H(DF): p	4.55(2): 0.073	**6.08(2): 0.048**	**6.2(2): 0.045**

In Kaneohe Bay, tumored turtles did not flinch significantly more often than healthy turtles overall (Kruskal-Wallis; H=0.20, DF=1, p=0.658), nor did tumored turtles flinch significantly more often than healthy animals given any particular foraging mode utilized by *T. duperrey* (Table 6). T-type feeding bites never engendered a flinch response from any turtle; healthy turtles flinched significantly less often when experiencing C-type bites as opposed to S-type bites (Table 6).

Table 6. Turtle flinches recorded for different foraging modes in Kaneohe Bay, Oahu Island, Hawaiian Islands

	Median bites (% of total bites) employed by *Thalassoma duperrey*		Kruskal-Wallis: H(DF): p
Turtle Condition	S-type	C-type	
Tumored	0.38	0.12	0.66(1): 0.417
Healthy	0.29	0.0	**4.57(1): 0.032**
Kruskal-Wallis: H(DF):	0.00(1): 0.966	1.05(1): 0.305	

Resting survey

One hundred eighteen minutes were spent in observations of turtle resting. Eighteen resting episodes were recorded, involving 5 turtles (Table 7).

Table 7. Observations of Turtle Resting Sites in Kaneohe Bay, Oahu Island, Hawaiian Islands

Reef Site	**Tumor Score**	**Turtle I.D.**	**N**	**Sex**	**Duration (x ± s.d.) in seconds**
42	1	42	8	Male	329 ± 60
42	0	20	1	Male	420
42	0	99	7	Male	360 ± 60
42	0	98	1	Undetermined	751
MR	0	97	1	Undetermined	694

Barnacle survey

In Kaneohe Bay, twenty turtles, 14 of them (70.0%) with GTFP tumors, were surveyed for skin barnacle densities. Barnacle load did not differ significantly between individual turtles (Kruskal Wallis; H=19.00, DF=19, P=0.457), and did not differ by geographic location at which the turtles were captured within the Bay (Kruskal Wallis;

H=0.32, DF=1, P=0.569). Barnacle densities did not correlate with the individual turtle's size (Pearson's correlation = -0.336, p=0.148), which averaged 57.7 +/- 9.6cm (mean +/- st. dev.), and ranged from 49.9 to 70.9 cm straight carapace length. Barnacle densities were highest in the tail region of the turtle, and greater on rear flippers and the neck than on the front flippers (Tables 8, 9). Barnacle densities were greater on healthy turtles than on turtles of tumor score 1 (Tables 8, 9).

Table 8. Two-way ANOVA of Barnacle density by Tumor Score (TS) and Location (L) of barnacles on turtle in Kaneohe Bay, Oahu Island

Source of variation	Sum of Squares	Degrees of Freedom	Mean Squares	F-statistic	P-value
Factor Tumor Score	1.417	2	0.708	5.438	**0.007**
factor Location	1.544	3	0.515	3.951	**0.012**
TS x L interaction	0.614	6	0.102	0.785	0.585
Error	7.815	60	0.130		
Total	11.389	71	0.160		

Table 9. Tukey's post-hoc comparison of barnacle densities on different turtle body locations (FFL=Front flippers, RFL=Rear flippers, T=Tail, H=Head, TS=Tumor Score per Table 1) in Kaneohe Bay, Oahu Island

Comparison	**Diff. of Means**	**SE**	**q**	**Table value (α=0.05)**	**Conclusions, p≤0.05**	
FFL x RFL	0.156	0.035	4.403	3.737	Reject H_0:	**RFL>FFL**
FFL x T	0.445	0.035	12.552	3.737	Reject H_0:	**T>FFL**
FFL x H	0.133	0.035	3.750	3.737	Reject H_0:	**H>FFL**
RFL x T	0.289	0.035	8.149	3.737	Reject H_0:	**T>RFL**
RFL x H	0.023	0.035	0.653	3.737	Accept H_0:	RFL=H
T x H	0.312	0.035	8.802	3.737	Reject H_0:	**T>H**
TS 0 x TS 1	0.321	0.085	3.772	3.399	Reject H_0:	**TS 0 > TS 1**
TS 0 x TS >1	0.202	0.085	2.377	3.399	Accept H_0:	TS 0 = TS >1
TS 1 x TS >1	0.119	0.085	1.395	3.399	Accept H_0:	TS 1 = TS >1

Confirmation of Symbiotic Relationship

Twenty-one *T. duperrey* were collected from the Reef 42 cleaning site in Kaneohe Bay. The size of fish collected ranged from 7.8 to 13.0 cm standard length, averaging 10.8 +/- 1.7 cm (mean +/- st. dev.). Six of these fish (29%) were cleaners, as indicated by the presence of parasitic turtle skin barnacles among their gut contents. The cleaners averaged 11.6 +/- 1.1 cm, and were not significantly smaller or larger than the non-cleaners, which averaged 10.4 +/- 1.7 cm (two tailed t-test, DF=15, t stat=1.834, p=0.087). Gut contents that contained parasitic skin barnacles were generally comprised of skin barnacles and little else.

Survey of Dive Tour Operators

Fifteen dive tour operators and 82 University of Hawaii academic research divers were polled in order to ascertain the location and seasonality (if any) of cleaning sites around the islands. This poll yielded the locations of four cleaning sites on Oahu, in addition to the three known from Kaneohe Bay. In addition, four sites were reported from the Hawaii Island, five from Maui I., two from Lanai I., and six from Kauai I. (Figure 1). No seasonality of cleaning sites was noted by any of the survey participants.

Table 10. Summary of fish species, feeding habits and flinch rate at all sites (K=Kaneohe Bay, Oahu H=Honokowai, Maui; L= "Turtle Haven", Lanai; Ha=Hanauma Bay, Oahu, Ho=Honokohau, Hawaii I., M=Mauna Lani, Hawaii I., Hi = Leleiwi, Hilo, Hawaii I., NC=# bites taken not counted, *= only bites on skin or tumor counted, N/A=not available)

Cleaner Species	Feeding habits	Reference	Sites	Mean Flinch Rate(n)
Thalassoma duperrey	Predator benthic shelled organisms	Hobson 1974	K, H. L, Ha. M, Hi	K=0.15(593), H=0.03(38), M=0.18(11), Ha=N/A, Hi=N/A. L=N/A
Canthigaster jactator	Omnivore-coralline algae and hard bodied inverts.	Hobson 1974	K, H. Ha	K=0.50(2), H=0.36(36), Ha=N/A
Forcipiger flavissimus	Predator-tears off pieces of large benthic animals	Hobson 1974	H	H=0.30(143)
Chaetodon miliaris	Zooplanktivore, cleaner	Hobson 1974	K, H	K=0(N/C), H=0.05(113)
Ctenochaetus strigosus	Grazer- algae, diatoms, detritus, bacteria	Jones 1968	K, H, L, Ha, Ho, M. Hi	K=0(NC), H=0.005(421*), L=0(NC), Ha=0(NC), Ho=0(NC), M=0(NC), Hi=0(NC)
Pseudocheilinus octotaenia	Predator-benthic crustaceans	Hobson 1974	H	H=0.5(4)
Zebrasoma flavescens	Herbivore-benthic algae	Jones 1968	Ho, M	0(NC)
Centropyge potteri	Grazer-benthic algae and organic detritus	Hobson 1974	Ho	0(NC)
Acanthurus nigrofuscus	Herbivore-benthic algae	Jones 1968	Ho	0(NC)
A. nigroris	Herbivore-benthic algae	Jones 1968	M, Ho	0(NC)
A. nigricans	Herbivore-benthic algae	Jones 1968	Ho	0(NC)
A. triostegus	Herbivore-benthic algae	Jones 1968	Ho, M	0(NC)
juvenile *Scaridae*	Herbivore-benthic algae	Hobson 1974	K	0(NC)
Labroides phthirophagous	Cleaner-ectoparasites	Hobson 1974	K	0(NC)
Chromis hanui(?)	Planktivore	Hobson 1974	Hi	0(NC)

cleaning site within Kaneohe Bay, Oahu Island, Hawaiian Islands (Figure 2). Reef 42 is located at N 21°28.593', W 157°49.451', and "Mark's Reef" is located at N 21°27.486', W 157°47.867'. In addition, the vicinities of both cleaner stations used in the study were mapped in detail to a radius of approximately 50 m (Figures 3 & 4).

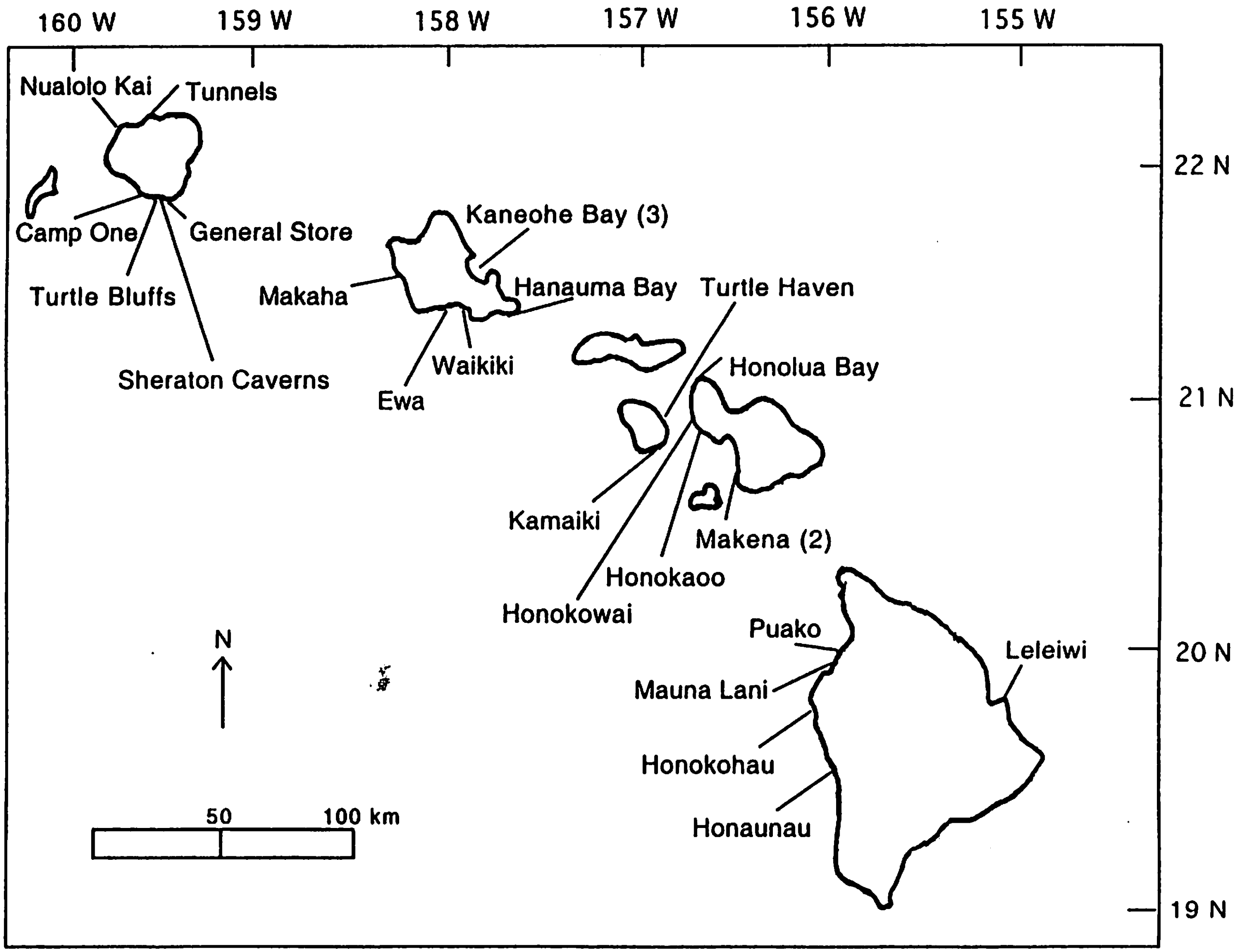

Figure 1: Location of *Chelonia mydas* cleaning stations in the Hawaiian Islands

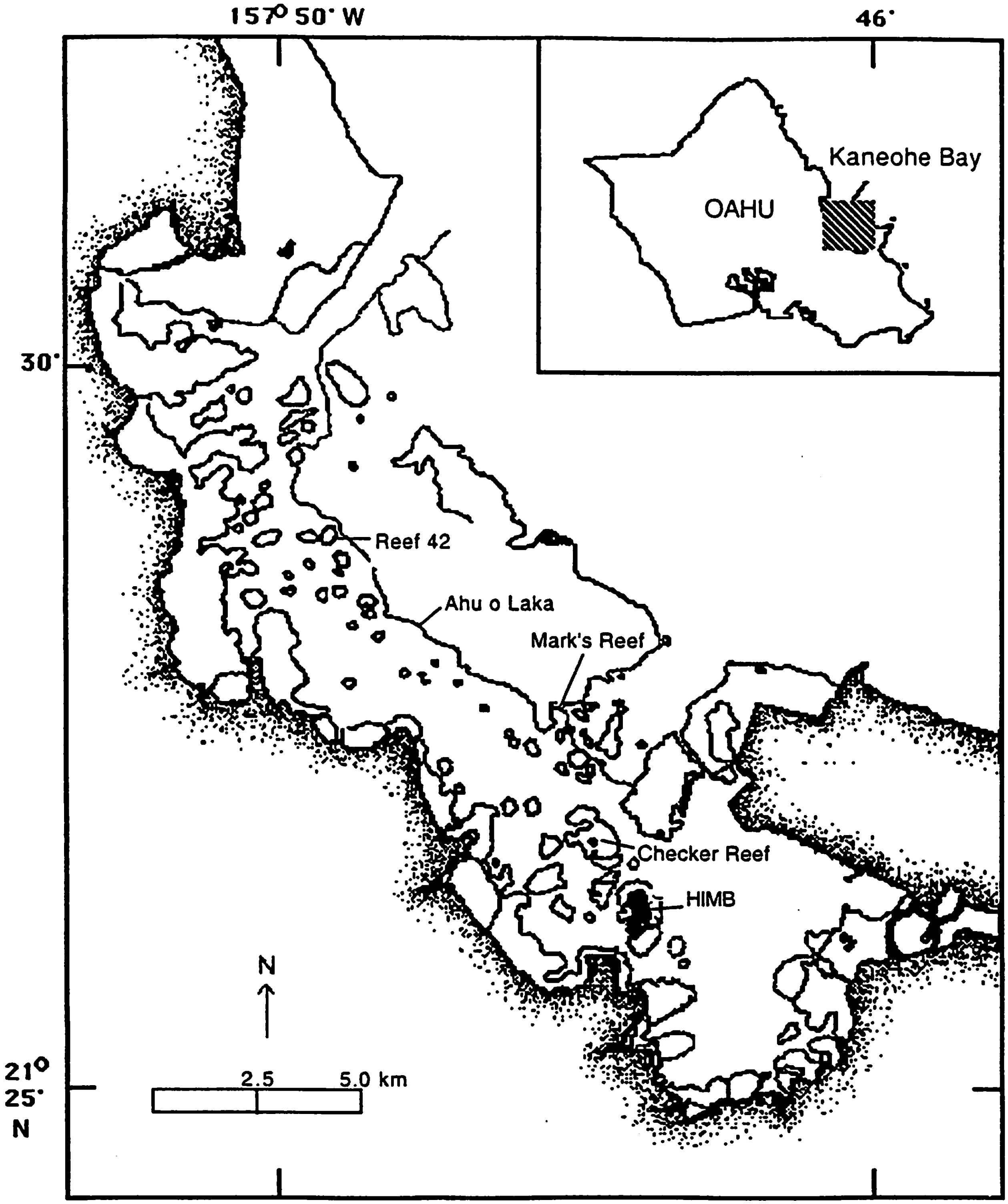

Figure 2: Study site locations in Kaneohe Bay, Oahu Island, Hawaiian Islands

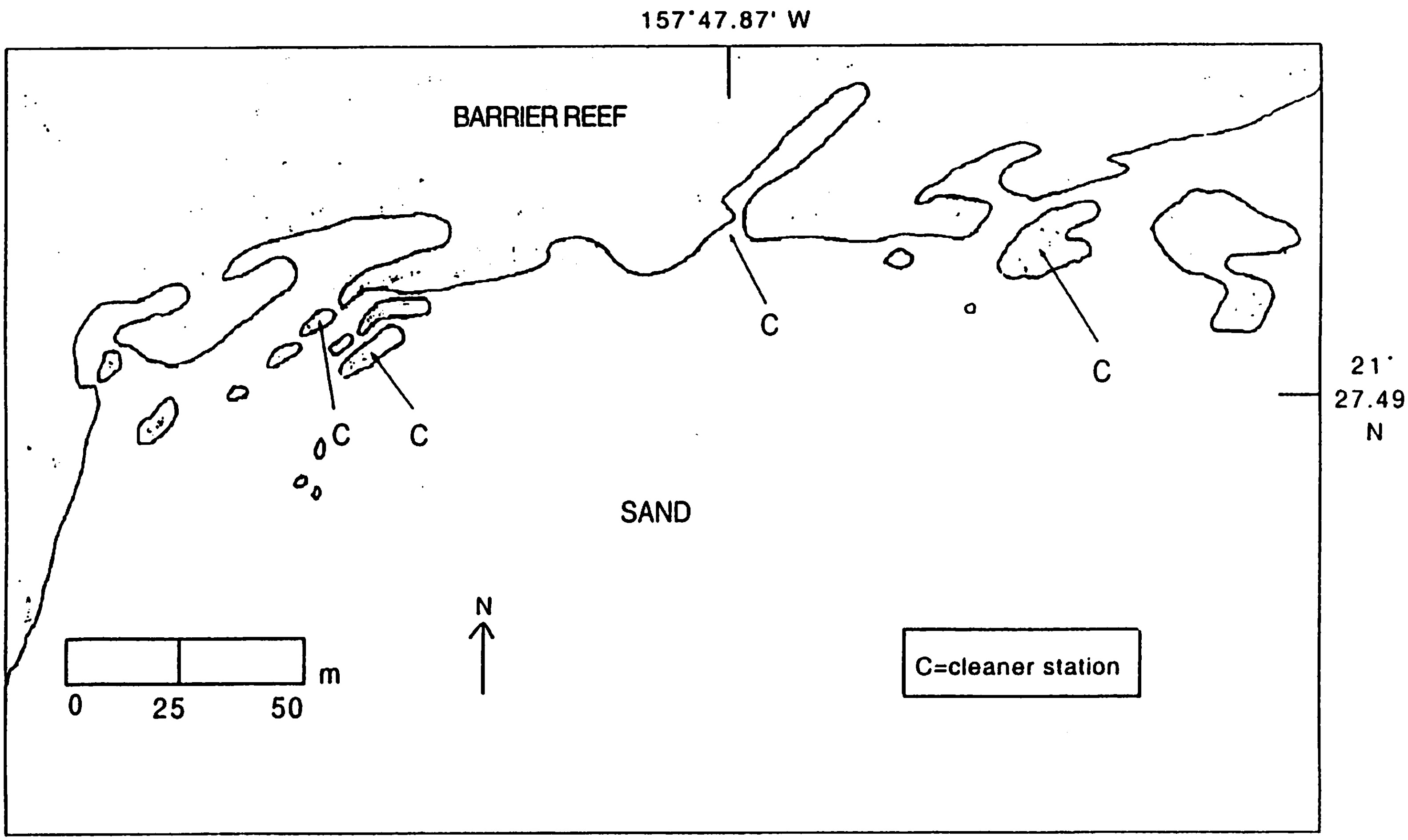

Figure 3: Location of cleaning stations at Mark's Reef, Kaneohe Bay, Oahu

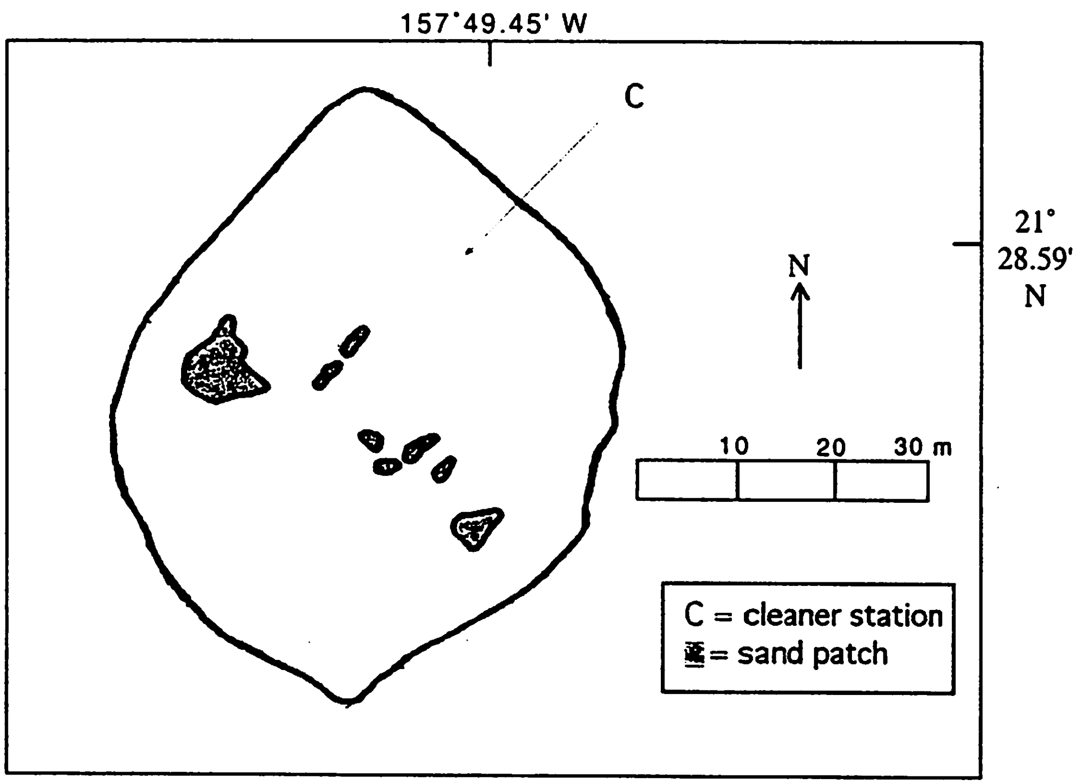

Figure 4: Location of cleaner station at Reef 42, Kaneohe Bay, Oahu Island

DISCUSSION

Symbiosis is a term that simply means, "living together," from the Greek *syn*, together, and *bioun*, to live (Friend and Guralnik 1957). There is some inconsistency in present-day biology as to how this term is used; some writers take the broad term "symbiosis" to include mutualism, commensalism, and parasitism (Wilson 1975), whereas others treat the word symbiosis as a synonym for mutualism (Immelmann and Beer 1989). Cleaning symbioses, in marine, terrestrial, and freshwater habitats, are often assumed to be mutually beneficial to the participants (Feder 1966, Hendler 1984, Poulin 1993, Mooring and Mundy 1996, Krawchuk 1997). In many cases however, this may be an overly simplistic view of the relationship (Losey 1979, Zander and Neider 1997, Grutter and Poulin 1998).

Symbioses between Hawaiian reef fishes and green sea turtles also are more complex than simple mutualistic systems. In fact, this study documents at least two different types of cleaning symbioses occurring between green sea turtles and Hawaiian reef fishes. Grazing symbioses, when herbivorous and detritivorous fishes remove algae from the turtle's shell (e.g. on the Kona coast of the island of Hawaii) seem to fit the classic "mutualistic cleaning interaction" assumptions. Non-grazing symbioses, characterized by omnivorous or carnivorous fishes removing invertebrates from the turtles skin (e.g. Kaneohe Bay and Hanauma Bay, Oahu I., Honokowai, Maui I.), may be mutualistic, or commensal, or fish may even be effectively parasitic.

Mutualistic grazing cleaning symbioses?

Cleaning stations inhabited primarily by grazers. such as Honokohau, and Mauna Lani, seem to have mutualistic interactions. The turtles likely receive a "tactile reward" (Losey 1987) as the grazers clean their shell. Turtle shells are sensitive (E. Jacobson, pers. comm.; J. Frazier, pers. comm.), and green sea turtles will correctly perform operant conditioning tasks for a "scratch reward" on their shell (S. Floyd, pers. comm.). The grazing fish at Honokohau and Mauna Lani benefit by exploiting a valuable food source in an area with high coral cover. At least eleven species of algae (Balazs 1980), as well as ostracods (T. Work, pers. comm.), are found growing on the Hawaiian green turtle's shell and skin. These algae may negatively affect the turtle's hydrodynamics, creating drag as the animal swims, therefore grazing of these algae would result in increased swimming efficiency and reduced energetic expenditure by the turtle. It is also possible that the grazing stations are an example of "sensory exploitation" by the cleaner fish (Losey 1979), cleaning is not advantageous to the turtle. and these symbioses would be of a commensal nature.

The lack of carnivorous cleaners at these sites is puzzling. A small number of *T. duperrey* have been seen cleaning turtles at the Mauna Lani site. Losey *et al.* (1994) and I found that *T. duperrey* individuals in Kaneohe Bay specialize at cleaning turtles, at least on a daily basis. Losey *et al.* (1994) estimated that it would take six turtles to feed one cleaner *T. duperrey*. Given that I observed six turtles at the Mauna Lani station simultaneously, it is reasonable to estimate that the population size is greater than six individuals. Perhaps this level of turtle density has only recently become high enough to provide a stable food source for a few *T. duperrey*. There may not be enough turtles to carry a sufficient load of barnacles at the Kona sites to support more than a few daily-specialist cleaners. An investigation of the gut contents of Kona *T. duperrey* cleaners in order to determine if they are daily specialists would certainly be worthwhile. Further study of these Kona coast cleaning sites might document the emergence of a cleaning station analogous to Kaneohe Bay, as turtle densities increase. Another explanation for the lack of carnivorous cleaning might be that, in the clear oceanic waters of the Kona Coast of the island of Hawaii, fouling organisms such as barnacles are not found in such high densities as in the nutrient rich waters of Kaneohe Bay. This hypothesis could be easily tested with a field survey of skin barnacle densities on Kona coast turtles.

Singularity of Kaneohe Bay cleaning symbiosis

I concur with Losey *et al.* (1994), who predicted that Kaneohe Bay, Oahu Island is a new kind of turtle cleaning symbiosis among those occurring in the Hawaiian Islands. A number of factors contribute to this singularity. First, grazers are present only a small amount of the time, as opposed to the general abundance of grazers cleaning turtles elsewhere in the Islands. The lack of grazing activity may be due to the inordinately high availability of alternate algal/detrital food sources in Kaneohe Bay, which has a long history of alga introductions and subsequent proliferation (Russell 1992, Russell and Balazs 1994, Hunter and Evans 1994). Alternatively, the paucity of grazers could result from the heavy fishing pressure experienced by fishes in Kaneohe Bay, where gill-netting is a common occurrence (JPZ pers obs). Second, the majority of the cleaning in Kaneohe Bay is performed by *T. duperrey*, as opposed to the grazer- and butterflyfish-dominated stations elsewhere in the Hawaiian Islands. Third, *T. duperrey* did not prefer turtles with tumors as do the non-grazing cleaners at Hilo and Honokowai. Finally, *T. duperrey* did not prefer the tumors over adjacent skin areas, as do the non-grazers at Honokowai and elsewhere in the Islands. *Thalassoma duperrey* is very common in Kaneohe Bay, and is an extremely opportunistic feeder (Hobson 1974). It would seem that in Kaneohe Bay *T. duperrey* have learned to recognize the skin barnacles as a food source and remove them while fostering cooperation with the turtle host.

I found that 29% of the *T. duperrey* in the vicinity of a cleaner station were cleaners, which agrees with Losey *et al.* (1994), who found that five of 15 fish sampled from a cleaner station in Kaneohe Bay were cleaners. New cleaning stations in Kaneohe Bay have arisen since the publication of Losey *et al.* (1994). Despite repeated research in the reef 42 area by the same National Marine Fisheries Service personnel who reported the initial symbiosis at MR, cleaning at reef 42 (Figures 2,4) was not seen until April of 1996 (pers obs). At Mark's Reef, the original cleaning site has now spread to several different locations in the immediate vicinity (Fig 3). The same unusual non-selective feeding by *T. duperrey*, the fishes not focussing on tumors as they do elsewhere in the state, is seen at all the sites in Kaneohe Bay. This, in addition to the evidence discussed by Losey *et al.* (1994) supports the idea that cleaning behavior shown by *T. duperrey* in Kaneohe Bay may be spreading by social transmission.

Three different feeding modes (S-, C-, and T-type; defined below) were displayed by *T. duperrey* in Kaneohe Bay, Oahu Island. Losey *et al.* (1994) suggest that "the wrasses have probably learned to recognize the barnacles as a food supply and how to remove this food in a manner that promotes cooperation and solicitation by the turtles." This may be the reason for the different modes of feeding by the wrasse. T-type bites, when the fish mouths the turtle without any real momentum or bending of the body, may provide a tactile reward to the turtle; they could be an example of "host stabilization" behavior (Potts 1973). These bites are most often taken on a comparatively lower food quality, yet sensitive area, the turtles' shell, and may serve to initiate posing by the host turtle. It may be the case that *T. duperrey* has learned to foster cooperation by not focussing their biting on the sensitive tumor and eye areas of the turtle, and by utilizing T-type bites as reward and/or "host stabilization behavior." Alternatively, T-type bites may be simply *T. duperrey* exploring the feasibility of the shell as a food source.

The S-type and C-type feeding bites are delivered with considerably more force than the T-type feeding bites. A bite was considered "S-type" when the fish closed its jaws on a parasite, or the turtle's skin or tumor tissue, and then thrashed its body back and forth, describing an S-shaped motion. A twisting or rotation of the body sometimes accompanied this bite, and the bite would cease only when the parasite or piece of tissue had apparently been removed. A C-type bite seemed to serve to remove parasites that were not as firmly attached to the turtle as those requiring an S-bite. The fish would bite with enough forward velocity such that its body formed a "C" shape upon contacting the turtle, but would not latch on and thrash about as it would in an S-type bite.

The S-type feeding mode was used least often by *T. duperrey* in Kaneohe Bay. This may be related to the fact that S-type bites caused more flinches from turtles than C-type bites (though the difference was not significant for tumored turtles). The wrasses may have learned to limit the number of S-type bites taken in order to minimize perturbation of the turtle hosts. Alternatively, perhaps S-type bites are only used when necessary to remove particularly difficult prey items from the turtle.

It seems reasonable to assume that an S-type feeding bite would remove a bigger piece of prey than a C-type bite. S-type bites were taken more often on turtles with GTFP tumors than on healthy turtles. Green turtles harbor numerous ectoparasites, including leeches, mites, trematodes, ostracods, and bacteria (Aguirre *et al.* 1994, T. Work pers. comm.). Green turtles with GTFP are immunosupressed (Aguirre 1995) and hence may be unable to fight off parasites; the tumored turtles would therefore have a higher parasite load than an animal with a healthy immune system. If an S-bite is more efficient at removing large quantities of food, it might "pay off" for the fish to risk turtle perturbation and loss of the food source in order to exploit the immediate availability of an abundance of calories. This would explain the higher rate of S-type bites on tumored, more highly parasitized turtles. Alternatively, perhaps larger or more difficult to remove prey are found on tumored turtles, and this is the reason for the high number of S-type bites. Feeding rates are highest in the posterior areas of the turtle, where barnacle densities are highest.

Parasitic cleaning symbioses?

The Kaneohe Bay cleaning interactions stand in stark contrast to other non-grazer dominated cleaning stations elsewhere in the Hawaiian Islands, where butterflyfish (Honokowai), *T. duperrey* (Lanai, Hanauma, Leleiwi), or *Canthigaster jactator* (Hanauma, Honokowai) predominate as non-grazing cleaners. These non-grazer stations fall into more than one category: the first is a parasitic interaction, as seen at Hanauma and Leleiwi, with fishes apparently driving hosts away from the cleaner station by focussing bites on the turtles' tumors and eyes. The second type of symbiosis, found at Honokowai and Lanai, is more difficult to explain.

Honokowai is another apparently unique cleaning station in the Hawaiian islands in that the main non-grazing cleaners are *Forcipiger flavissimus* and *Chaetodon miliaris*. *Ctenochaetus strigosus*, a grazer, focuses on skin and tumor areas of the turtles at Honokowai far more often than *C. strigosus* at other locations in the islands. All the cleaners at Honokowai focus almost exclusively on the tumors of the turtles, and the turtles flinch quite often, yet they do not leave the cleaning station. It seems clear that the fish derive some benefit (food) from the interaction, but whether the host is benefitting or suffering is unclear. The turtles at Honokowai and Lanai flinch far more often than the turtles at Kaneohe, and so may be adversely affected by the cleaning through increased stress or opening of wounds by the cleaner fishes. These Honokowai and Lanai hosts pose and remain in the area despite the flinching. If one assumes that the turtles are behaving optimally, then their reluctance to leave a cleaning station may mean that they are deriving more benefit than detriment from parasite removal or possibly tumor amelioration. Interestingly, P. Bennett *et al.* (1999) have photographically documented 21 GTFP regression cases (=32% of infected turtles) at Honokowai, Maui; perhaps the fishes contribute to this tumor amelioration. Surgical removal of GTFP tumors performed in Florida has been shown, in a few individual turtles, to be a successful treatment with no subsequent tumor proliferation for at least eight years (L. Herbst, pers comm). The ratio of benefit to detriment at stations such as Honokowai and Lanai may change on a daily, or even hourly, basis, depending on the behavior of the participants.

Future directions

Cleaning symbioses in the Hawaiian Islands are found predominantly on leeward shores of the islands (Fig 1). This may be due to the fact that more SCUBA diving is done on these sheltered leeward shores, and therefore more stations were reported from these areas. A comprehensive survey of the exposed sites of the islands could reveal the locations of yet more turtle cleaning stations. Turtle cleaning stations are often found near some topographic anomaly, like a large coral head or bowl-like depression atop a spur-and-groove reef finger (Balazs 1980, JPZ pers. obs.). This may be because the topographic relief serves as an easily recognizable landmark, increasing the return rate of the turtles to the cleaner station after they ascend to the surface to breathe, or leave to forage. Alternatively, such topography may provide shelter to cleaning reef fish if a threatening predator appears. My data in Kaneohe Bay, as well as the diver survey, indicate that there is no seasonality to cleaning symbioses in the Hawaiian Islands. An intense study of cleaning stations conducted during the green turtle breeding season (when adult females and males migrate up to French Frigate Shoals to mate and lay eggs), for comparison with the rest of the year, might turn up some heretofore unnoticed small differences in any of the variables explored in this paper. It is not the juvenile *T. duperrey* which clean, as it is with many species of opportunistic cleaner, though juvenile *T. duperrey* do function as fish cleaners on the Kona coast of Hawaii Island (Hobson 1972).

Examination of the resting data revealed an interesting fact: of the turtles known to be male, the mean resting duration was considerably lower than that of the turtles known to be female (Table 7). This may be an artifact of small sample size, or may actually show relation to turtle size (or some other factor) and not sex necessarily, but might easily be disproved or supported by minimal future investigation. As resting duration is effectively a function of the frequency with which the turtle leaves the resting site to breathe before returning to rest, this may indicate some difference in adult male oxygen usage or metabolic rate as compared with females or juvenile animals. Resting interactions indicated that individual turtles show fidelity to a particular resting site, at least over the course of a few hours, which agrees with anecdotal observations reported from Honokowai (U. Keuper-Bennett, pers. comm.).

Comparative cleaning sites

Several of the cleaning sites identified in the aforementioned survey were selected for further study. A total of 157.5 min of videotape, 54.7 min from Honokohau, Kona Coast, Island of Hawaii; 43.0 min from off the Mauna Lani, Kona Coast, Island of Hawaii; 4.6 min from Leleiwi, Hilo, Hawaii; 19.7 min from Hanauma Bay, Oahu; 12.1 min from "Turtle Haven", East Lanai; and 37.8 min from Honokowai, West Maui; were analyzed.

At the Mauna Lani, Kona coast, Hawaii Island sites, grazers observed cleaning were: *Ctenochaetus strigosus*, *Acanthurus triostegus*, *A. nigroris*, and *Zebrasoma flavescens* (Table 10). *Thalassoma duperrey* was observed taking 11 cleaning bites, at an overall rate of 1.06 bpm. Two flinches were recorded, yielding a flinch rate of 0.18 flinches/bite taken (Table 10). Six individual turtles were present at the cleaning site, and none of them had visible tumors. Green turtle fibropapillomatosis has never been observed along the Kona coast of the island of Hawaii (Balazs et al 1996).

At Honokohau, Kona coast, Hawaii Island, *Zebrasoma flavescens*, *Ctenochaetus strigosus*, *Centropyge potteri*, *Acanthurus nigricans*, *A. triostegus*, *A. nigroris*, and *A. nigrofuscus* were observed cleaning (Table 10). Eight individual turtles were present at this cleaning site, and none of them had visible tumors. No flinches were recorded at this site (Table 10).

Four individual turtles were seen at Hilo, Hawaii Island; all had tumors. Three *T. duperrey* were observed biting at large flipper tumors of one heavily tumored turtle as it swam away from the reef and quickly out of the range of visibility. Another resting turtle with tumors was seen to flinch twice in response to bites by a *T. duperrey*, which took four bites before being chased off by a *Stegastes fasciolatus*. Interestingly, this *S. fasciolatus* and two *Chromis hanui* were each apparently defending portions of the turtle's shell as it rested. *Chromis hanui* was seen inspecting, and possibly feeding, on the shell of the turtle; shell feeding by *Ctenochaetus strigosus* was observed several times at the Hilo site (Table 10).

Acanthurus spp. and *Ctenochaetus strigosus* were observed grazing on three turtles at Hanauma Bay, Oahu Island (Table 10). A fourth, severely tumored turtle (TS=3 from Table 1), arrived on the cleaning station, and herbivores did not approach it, but both *Canthigaster jactator* and *T. duperrey* bit at the turtle's tumors repeatedly. The turtle did not pose, but flinched seven times and swatted at the fishes three times as it swam over the reef. The number of bites taken by each species could not be recorded due to poor videotape quality.

At "Turtle Haven," East Lanai Island, fish species observed cleaning were *Ctenochaetus strigosus*, *T. duperrey*, and *Acanthurus spp* (either *xanthopterus*, *blochii*, or both) (Table 10). None of the turtles had obvious tumors, and a dive tour operator indicated that he had been diving around Lanai Island since 1984, and had never observed a turtle with signs of GTFP. Five turtles were observed being cleaned at East Lanai. One turtle, which had either an extremely small tumor or a barnacle (unidentifiable white spot) at the posterior corner of its left eye, flinched six times in a span of seven minutes of cleaning by *T. duperrey*. Each flinch occurred after *T. duperrey* approached or bit at one of the turtle's eyes; however, the turtle remained at the site and continued to pose for cleaning. Number of bites taken by *T. duperrey* could not be recorded due to poor videotape quality.

At Honokowai, West Maui Island, only turtles with GTFP tumors were observed engaged in cleaning interactions. Of 14 turtles sighted, 10 (71%) were afflicted with GTFP. Of 755 recorded bites, 421 were taken by the grazer *Ctenochaetus strigosus*. Only grazing bites that landed on the skin or tumor tissue of the turtle were counted. The total numbers of non-grazer cleaner fish bites taken were: 143 by *Forcipiger flavissimus*, 113 by *Chaetodon miliaris*, 38 by *T. duperrey*, 36 by *Canthigaster jactator*, and four by *Pseudocheilinus octotaenia* (Table 10). Fishes at Honokowai were found to feed more commonly on tumored tissue than would be expected based on an ideal free distribution of bites between tumored and non-tumored tissues (randomization test vs. estimation index in Methods section $p<0.01$ at 10,000 iterations). In order to test for a difference between Kaneohe Bay and Honokowai, the rate at which fish in Kaneohe Bay fed on tumors was assumed to be the "rule" by which Honokowai fishes distributed their feeding bites (see Methods section). Given this null hypothesis, Honokowai fishes fed far more commonly on tumored tissues than expected ($p<0.01$ at 10,000 iterations). Turtles at

Honokowai were cleaned by non-grazing fishes at a significantly higher rate (bites-per-minute cleaning) than turtles in Kaneohe Bay were cleaned by *T. duperrey* (Kruskal-Wallis test, H=9.85, DF=1, p=0.002). *Thalassoma duperrey* feeding rates did not differ between Honokowai and Kaneohe Bay (two-tailed t-test, t=0.473, DF=7, P=0.325). The tumored turtles at Honokowai were not found to flinch significantly more often (flinches per bite taken) than tumored turtles in Kaneohe Bay (Chi-squared test, G=0.839, p=0.360); however, a single Kaneohe Bay turtle accounted for 55% of flinches in the tumored population of the bay. If this animal, which was severely tumored (TS=3 from Table 1) and in all likelihood blind, is excluded from the data set, Honokowai turtles flinched significantly more often than tumored Kaneohe Bay turtles (Chi-squared test, G=6.80, p=0.009).

CONCLUSIONS

1. Cleaning symbioses between green sea turtles, *Chelonia mydas*, and reef fishes are common throughout the Hawaiian Islands.
2. Kaneohe Bay is a unique cleaning environment, characterized by a) a paucity of grazers, b) *T. duperrey* as the main cleaner, and c) *T. duperrey* feeds primarily on skin barnacles, not turtle tumors.
3. *Thalassoma duperrey* in Kaneohe Bay feeds most rapidly on the rear areas of the turtle, which have the greatest density of skin barnacles.
4. *Thalassoma duperrey* in Kaneohe Bay displays three different modes of feeding, and turtles react to each of these modes of feeding differently.
5. Honokowai, West Maui I. is a unique cleaning environment, characterized by a)fishes cleaning tumors almost exclusively, and b) *Forcipiger flavissimus*, *Chaetodon miliaris*, and *Ctenochaetus strigosus* as the main cleaners.
6. Cleaning stations on the Kona coast of Hawaii I. are characterized by an abundance of shell grazing fishes and a paucity of skin cleaners.
7. Parasitic interactions between sea turtles and *T. duperrey* and *Canthigaster jactator* occur at Hilo, Hawaii I., and Hanauma Bay, Oahu I.

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